DUPLICATE:

Accession Number	400149
Borrower	Peter Paras Jr.
Organization	1632
Phone	308-8340
Request Date	06/17/2002
Document Type	Journal article
Journal Name	HYDROBIOLOGIA
volume	298
Issue	1-3
Pages	73-81
Year	1995
Source	EYM
Delivery Date	06/21/2002
Delivered Via	FAX

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Mating behavior and time budget of an androdioecious crustacean, *Eulimnadia texana* (Crustacea: Conchostraca)

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Key words: androdioecious crustacean, *Eulimnadia texana*, behavior, mating

Abstract

The clam shrimp, *Eulimnadia texana* (Crustacea, Conchostraca), is found in freshwater ephemeral environments throughout the United States. Individual clam shrimp of this species are either hermaphroditic or male, a relatively rare mating system for animals known as androdioecy. Comparison of sex ratios between four neighboring populations of *E. texana* in Southern New Mexico showed wide variation in the ratio of males to hermaphrodites with males making up as much as 42% of some populations and not occurring at all within others. Since little is known about the behavior of this species, an ethogram and time budget were prepared based on observations of laboratory populations. Males attempt to clasp hermaphrodites prior to mating. Precopulatory mate guarding occurs in this species. Outcrossing generally occurs during mate guarding and after the hermaphrodite molts. Hermaphrodites, however, seem to control the mating process. Successful mating by males never occurred if the hermaphrodite struggled with him; hermaphrodites will self in the presence of males.

Introduction

The clam shrimp, *Eulimnadia texana* (Crustacea: Conchostraca) is found across North America (Sassaman, 1989). This species inhabits small ephemeral ponds that typically appear due to spring and summer rains. The puddles dry up and the eggs remain dormant until the puddles reform. *Eulimnadia texana* is androdioecious, a rare situation in animals in which a species has both male and hermaphroditic individuals (Sassaman & Weeks, 1993). Hermaphrodites can self or outcross with a male, but they cannot exchange sperm with other hermaphrodites (Sassaman & Weeks, 1993). The body of the clam shrimp is encased within a translucent, carapace through which most organs are visible. Clam shrimp have numerous pairs of legs which are used for feeding. *Eulimnadia texana* feeds primarily on algae though it will eat other types of detritus when algae is limited (Medland, 1989).

Pronounced sexual dimorphism allows easy identification of males and hermaphrodites. In the males, the first two pairs of thoracic appendages have been modified into claspers for grasping the hermaphrodite during outcrossing. Absence of such an adaptation pre-vents hermaphrodites from outcrossing with one another (Sassaman & Weeks, 1993). The hermaphrodite's unfertilized eggs lie in paired ovaries along its digestive tract and are visible under a microscope. When fertilization occurs, the eggs move into a brood chamber where they are contained in a mucous mass between the hermaphrodite's dorsum and the carapace. The eggs are visible to the naked eye and aid in sexing the clam shrimp.

Research involving this species has focused primarily on the genetics and theoretical implications of this mating system (see Strenth, 1977; Sassaman, 1989; Sassaman & Weeks, 1993; Otto *et al.*, 1993). Sassaman & Weeks (1993) have shown that sex determination occurs at a single autosomal locus and that individuals are either monogenic hermaphrodites (those which produce only hermaphroditic offspring), amphigenic hermaphrodites (those which produce both male and hermaphroditic offspring), or male. Monogenic individuals are homozygous dominant at the autosomal locus, amphigenic individuals are heterozygous, and males are homozygous recessive (Sassaman & Weeks, 1993). This system is very similar to the reproductive systems of many Notostracans (Sassaman, 1991). Due

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to the nature of sex determination, populations typically consist of many more hermaphrodites than males (Sassaman, 1989; pers. obs.).

Behavioral information on *E. texana* is largely unavailable in the primary literature and would be a useful supplement to ongoing evolutionary and genetic studies which are examining the significance of sex, inbreeding and outcrossing. To that end, this contribution provides an account of male and hermaphrodite behavior in the form of an ethogram, time budget and detailed descriptions of mating behavior.

Methods

Study populations

Four populations of *E. texana* have been identified just northeast of the Doña Ana Mountains, 40 km NNE of Las Cruces, Doña Ana County, New Mexico. These populations are all located within 4 km of one another. Three of the populations are located along the access road to the New Mexico State University College Ranch, next to South Well. These populations are referred to as SWP3, SWP4 and SWP5 (South Well puddle populations). Each of these sites consists of a distinct depression less than 10 meters in length and with a depth no greater than 1 meter at the lowest point. SWP5 is almost directly across a dirt road, 35 m from SWP3. SWP4 is 130 m west of SWP3 on the same side of the road. There is sparse vegetation immediately around these puddles predominantly consisting of various grass species. There is little to no vegetation within the puddles themselves. These sites typically fill with water at least once every year as a result of summer rainfall and remain filled for three days to several weeks depending upon further water inputs (pers. obs.). Other than *E. texana*, these sites are also occupied by populations of *Scaphiopus couchii* tadpoles, which hatch well after the clam shrimp mature (and thus do not present a severe predation problem) and are also used as watering holes by cattle (pers. obs.).

The fourth population occurs within the playa portion of the NSF Long-Term Ecological Research site on the New Mexico State University College Ranch (LTER Playa), approximately 4 km west of the other three sites. The playa encompasses a 12-ha basin (Creusere & Whitford, 1976). The LTER Playa has considerably more vegetation than the SWP populations, including *Prosopis, Panicum, Amaranthus, Hymenoxis,* and *Helianthus* (MacKay *et al.,* 1990).

The ecology and population dynamics of this site have been studied quite extensively (see Creusere & Whitford, 1976; Medland, 1989; VanVactor, 1989; MacKay *et al.,* 1990 for an overview). This site receives an average rainfall of 210 mm annually (MacKay *et al.,* 1990). The majority of this precipitation (55%) is attributed to convectional rainstorms during the late summer months (VanVactor, 1989; MacKay *et al.,* 1990). The site is relatively level and does not flood as often as the SWP populations, typically flooding once every three to ten years and remaining flooded for several weeks (MacKay *et al.,* 1990). In addition to *E. texana,* MacKay *et al.,* (1990), indicate that this site is also inhabited by the tadpole shrimp, *Triops longicaudatus,* and fairy shrimp species, *Thamnocephalus platyurus* and *Streptocephalus texanus* (D. Belk indicates that the report of *S. texanus* populations within the LTER Playa is likely a misidentification of a mixed population of *S. mackini* and *S. dorothae*). The life cycles of these species all overlap (MacKay *et al.,* 1990). Cattle have not been allowed within the site since 1972 (MacKay *et al.,* 1990).

General sampling and rearing methods

Numerous samples of the first 1–2 cm of soil were collected from each study site; soil within each site was mixed to ensure randomness. Sample populations were established in the laboratory by placing 250 ml soil samples in plastic mouse cages (30 cm × 12 cm × 15 cm) and hydrating them with 4 liters of aged tap water. The tanks were kept on a 24 hour light cycle using incandescent bulbs in reflectors to maintain summer-like temperatures of approximately 30 °C and were supplemented with tadpole food pellets until algal growth was initiated. Clam shrimp hatched within approximately 24 hours of wetting. Tadpole shrimp, *Triops longicaudatus,* also hatched from the same soil samples and were removed from the tanks as soon as possible to prevent predation.

Sex ratio calculations

Sex ratios were calculated for all four populations. Ten tanks were set up from each population (40 tanks total) using the methods just outlined. Sex was determined for every individual hatching within a tank. Sex ratios were computed following the procedures outlined in Sassaman (1989) as soon as sexual dimorphism was apparent (approximately three days after hatching). Comparisons of total viable eggs per 250 ml soil sam-

ples were made between populations. The number of eggs initially contained within samples is unknown.

Ethogram

Initial observations of behavior were compiled into an ethogram of clam shrimp behavior following the guidelines outlined in Martin & Bateson (1993).

Clam shrimp time budget

The LTER Playa population was the only population used for the remainder of the study due to the availability of information on population dynamics for this site under field conditions. Individual LTER Playa clam shrimp were uniquely marked using a small dot of Testers enamel paint. Clam shrimp molt from the inside of the carapace so paint marks are not lost with subsequent molts and provide a fairly permanent means of identification. Though clam shrimp can be sexed within three days of hatching, they cannot be marked for individual identification until five days after hatching when the carapace no longer collapses when paint is applied.

Sample groups were established in the laboratory and housed in plastic mouse cages. The bottoms of the cages were lined with 1 cm of 'clean' sand (i.e., sand free from Branchiopod eggs). Groups were composed of seven hermaphrodites and three males to reflect natural population sex ratios (see Results). The tanks were monitored using instantaneous scan sampling techniques as described by Altmann (1974). During each scan, the behavior of each clam shrimp was recorded during that moment in time. The order in which the clam shrimp were scanned was determined haphazardly based upon the order in which individuals came into view. Each tank was scanned six times a day at one hour intervals until less than half of the individuals (4 clam shrimp) remained within the sample population. Clam shrimp that died within the first two days of scanning were replaced with clam shrimp of the same sex and hatch date. Three control tanks were set up with the same sex ratios as the sample tanks but with minimal handling of the clam shrimp and no paint marking to determine whether handling and marking techniques had an adverse effect on life span.

Mating behavior

Other behavioral observations of *E. texana* were conducted using the focal animal technique outlined

Table 1. Sex ratios and number of viable eggs hatching within four populations of an androdioecious clam shrimp *Eulimnadia texana* from 250 ml soil samples.

Population	# of tanks	$\bar{x}\pm$s.d. clam shrimp	Total # of ind. hatched	Percentages herm.: males
LTER	10	17±7.2	170	70:30
SWP3	10	37±8.8	374	100:0
SWP4	10	34±5.0	342	60:40
SWP5	10	30±7.6	328	58:42

by Altmann (1974). Groups consisting of either a male and a non-gravid hermaphrodite, two males and a non-gravid hermaphrodite, or two non-gravid hermaphrodites and a male, were collected from rearing tanks and isolated in a plastic 'dixie' cup containing 125 ml of aged tap water. Pairs were observed using focal animal observation techniques for two hours and all interactions were recorded. If the two hour observation was complete and either outcrossing or selfing appeared to be eminent, the observation was extended to include observation of egg fertilization. No observation ever lasted longer than 2 hours and 25 minutes. Each focal animal was only used once.

Analysis

Data are presented as means (±sd). For statistical procedures, an α level <0.05 is considered significant throughout this study.

Results

Sex ratios

The sex ratios for the four populations are presented in Table 1. In SWP4, SWP5, and the LTER population, sex ratios were skewed in favor of hermaphrodites. No males were ever found in the SWP3 population. Table 1 also provides the average number of clam shrimp hatching from a 250 ml soil sample for each population. There is no significant difference in total viable eggs hatching between the SWP3, SWP4 and SWP5 populations ($\chi^2=3.19$, $df=2$, $P>0.1$). The LTER Playa population had a significantly lower number of eggs hatch, however, when compared to the three puddle populations ($\chi^2=81.9$, $df=3$, $P<0.001$).

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Ethogram

The major types of behaviors observed in initial observations are listed and described in Table 2. Behavioral categories have been broken down into those common to both reproductive forms, those specific to hermaphrodites, and those specific to males.

Clam shrimp time budget

Tanks were scanned over a period of 11 days for a total of 7 hours and 33 minutes of observations. Time budgets were computed for both males ($N=12$) and hermaphrodites ($N=28$) using the methods outlined in Martin & Bateson (1993). These results are summarized in Fig. 1. No distinction was made between feeding and swimming behaviors because the two occur simultaneously. These activities were the primary behaviors for both sexual forms.

The reproductive status of the hermaphrodites was recorded during each scan. Hermaphrodites were gravid 72% of the observation time. Hermaphrodites appear to dig burrows and may drop their clutches underground. On several occasions, males were seen entering burrows, but I never saw males digging their own. In six instances, males were seen clasping gravid hermaphrodites just prior to egg laying. This may be a form of pre-mate guarding.

Mortality rates were calculated for both the scan tanks and the control tanks. There was no difference in mortality rates between the two tank types ($\chi^2=1.28$, $df=1$, $P>0.2$). Pooling all tanks, male mortality was higher than that of hermaphrodites ($\chi^2=4.51$, $df=1$, $P<0.05$), especially starting on day 8 of life (Fig. 2). On average, hermaphrodites lived 50% longer than males. Each population was initially set up with a 3:7 ratio of males to hermaphrodites. By the end of the observations, there was a 1:4 ratio in each of the scan tanks. Pennak (1989) reported that Eubranchiopoda males typically die within an hour after outcrossing. This was not true for *E. texana* and probably not for other Eubranchiopoda as well (Belk, pers. comm.).

Clam shrimp mating behavior

During focal animal studies ($N=178$ groups), outcrossing occurred 95 times (53%), selfing occurred 20 times (11%) and no fertilization was evident either due to selfing or to outcrossing in 63 of the observations (35%) (Fig. 3). In 46 of these cases, no contact was seen between the male and the hermaphrodite during the two hour observation period. In all other cases, the male periodically clasped the carapace of a non-gravid hermaphrodite for several seconds at a time (first clasping by males; $\bar{x}=8\pm10.2$ min after isolation; range 0–35 min; $N=132$). Whenever the hermaphrodite struggled, the male released his hold and outcrossing did not occur ($N=37$). At other times the hermaphrodite did not struggle when clasped by the male, but instead, passively allowed the male to push it around the cup ($N=95$). The hermaphrodite's legs would continue to beat, suggesting active feeding, but it's antennae would remain motionless, suggesting that the male was providing all active locomotion for the pair (for definitions of 'swimming' and 'feeding' see Table 1). This behavior was always a precursor to outcrossing. The average pre-outcrossing clasp time for these observations was 27 ± 36.8 min (range=2–120 min; $N=95$). Near the end of the clasping period, the male forced much of his lower body up into the hermaphrodite's carapace by the ovaries and began to make thrusting movements with the posterior portion of his abdomen ($\bar{x}=26\pm10.4$ thrusts; range=15–41 thrusts; counts made for 52 observations). In all cases ($N=95$), the eggs moved out of the ovary and up into the brood chamber while the male was thrusting, suggesting that this is when sperm transfer and fertilization occur. As soon as the eggs entered the brood chamber, the male released the hermaphrodite and outcrossing was assumed to have occurred. Male thrusting and egg movement are both visible under the microscope. In 94 of the outcrossings, hermaphrodite molting occurred prior to fertilization, ($\bar{x}$ molting = 11 ± 5.8 min prior to fertilization; range=6–20 min; $N=94$). In the 95th outcrossing, no molting was seen during the observation but the clasping male began to thrust into the hermaphrodite's carapace anyway and egg movement still followed.

In the 20 observations in which selfing occurred, the males performed periodic clasping of the hermaphrodite's carapace for several seconds at a time but the hermaphrodites always struggled and the males never clasped the hermaphrodites for extended periods of time (>1 min). Prior to selfing, the hermaphrodite lay motionless on the substrate for up to several hours ($\bar{x}=65.3\pm34.6$ min; range=13–120+ min; $N=20$). Molting occurred on average 12.1 ± 4.9 minutes prior to selfing (range=2–22 min; $N=20$) and then the eggs moved into the brood chamber. No male ever attempted to clasp these hermaphrodites after they had molted.

Table 2. Ethogram based upon observations of laboratory populations of the clam shrimp *Eulimnadia texana*

| Behavior	Description
Behaviors performed by both hermaphrodites and males:	
Feeding	Clam shrimp are filter feeders. Rapid beating of the legs creates a current pulling microscopic particles toward the clam shrimp. Clam shrimp feed almost constantly.
Lying on Bottom	Lying on the substrate at the bottom of the tank. The legs may or may not be still.
Molting	Process of shedding old exoskeleton.
Out of View	Individual clam shrimp not visible. Possibly burried in the substrate.
Struggling	Rapid movements of the body in an attempt to disengage a clasping male.
Swimming	Locomotion around tank using antennae. It is difficult to distinguish this behavior from feeding behavior because the two may occur simultaneously.
Hermaphrodite-only behaviors:	
Digging	Performed by gravid hermaphrodites only. The gravid hermaphrodite will dig in the substrate at the bottom of the tank. A hermaphrodite may dig continuously for up to several hours.
Dropping a clutch	Release of the eggs from the brood chamber. This may occur in the substrate after digging.
Male only behaviors:	
Aggressive interaction	An interaction between a male clasping a hermaphrodite and another male attempting to interfere with the pair. These interactions involve bodily contact between males, such as pushing.
Clasping	Male clasps the carapace of another clam shrimp with the first two pair of thoracic appendages. Outcrossing is always preceded by this behavior. Males also clasp other males, as well as gravid or unreceptive hermaphrodites at times.
Tagging Along	One male is clasped to a hermaphrodite and another male clasps onto him forming a 'train'.
Takeover	A male takes a hermaphrodite away from another male as a result of an aggressive interaction.
Thrusting	Male clasped to a hermaphrodite forces the lower portion of his body up into the hermaphrodite's carapace near the paired ovaries and makes pulsating motions. Sperm transfer is assumed to be taking place.
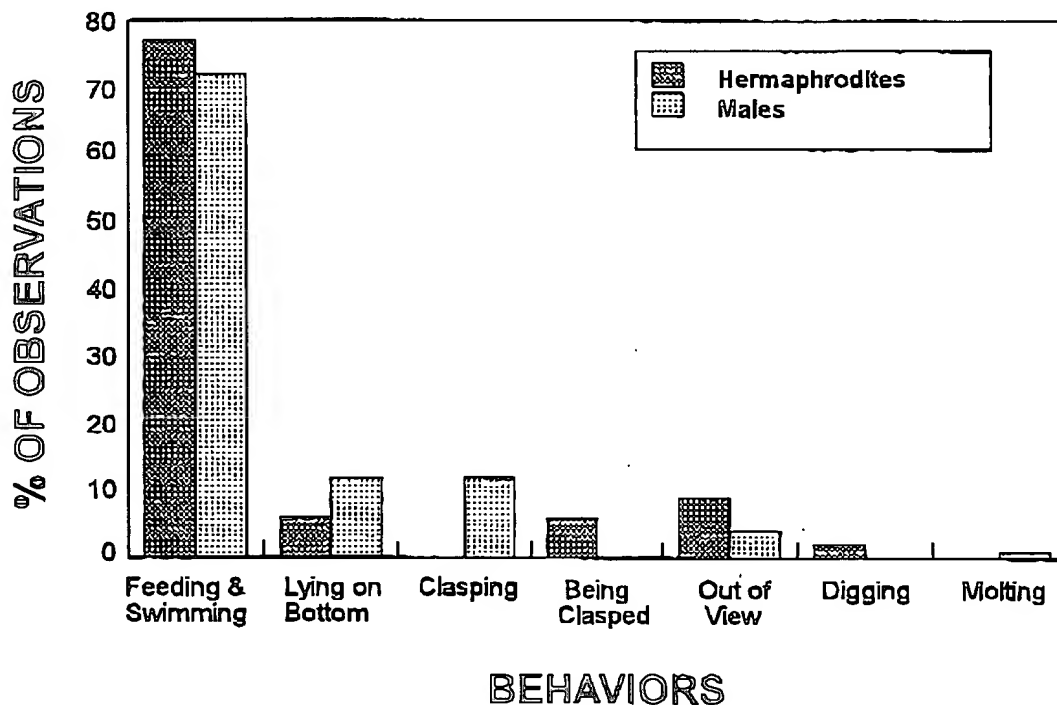
Fig. 1. Behavioral time budget for an androdioecious clam shrimp *Eulimnadia texana*. The bars indicate the average frequency of each behavior when compared to the total number of behaviors observed. Darker bars represent behaviors performed by hermaphrodites. Lighter bars represent behaviors performed by males.
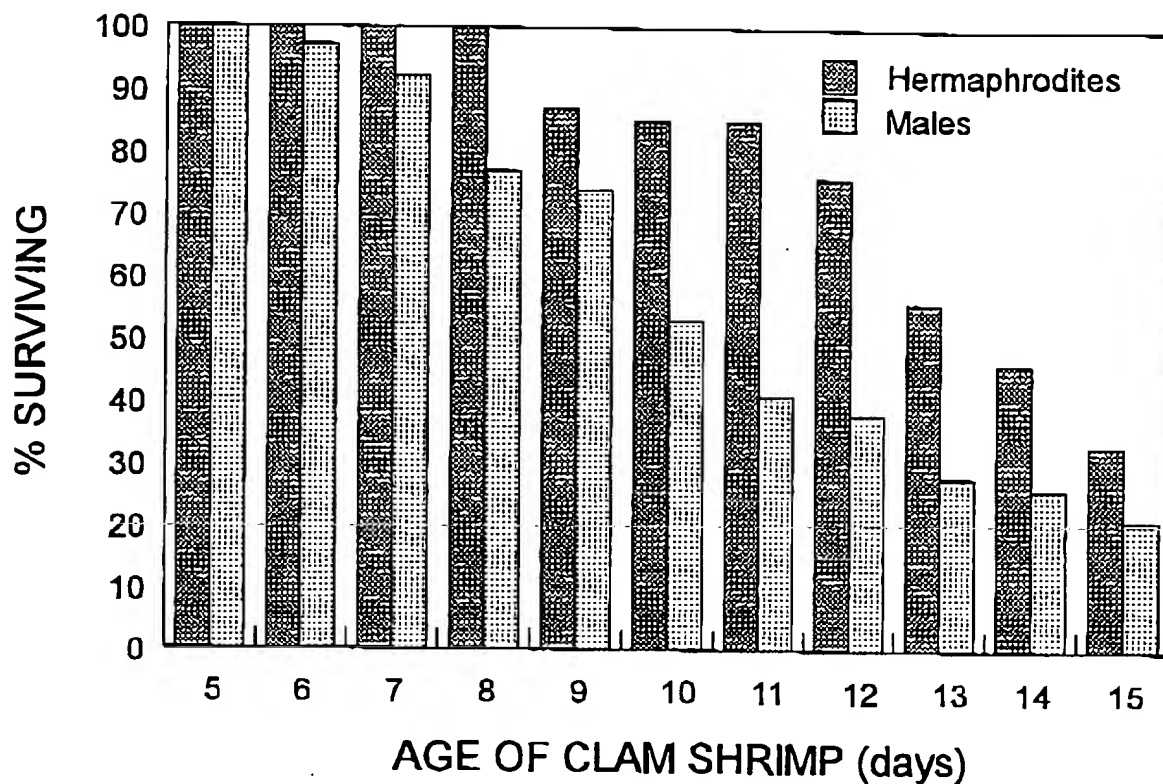
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Fig. 2. Comparison of hermaphrodite and male mortality rates for laboratory populations of the clam shrimp, *Eulimnadiu texana*. Populations were established when the clam shrimp were 5 days of age. *N* = 130 clam shrimp from 10 experimental and 3 control tanks. See text for explanation. The dark bars represent the percentage of hermaphrodites surviving each day (*N* = 91); light bars represent surviving males (*N* = 39).
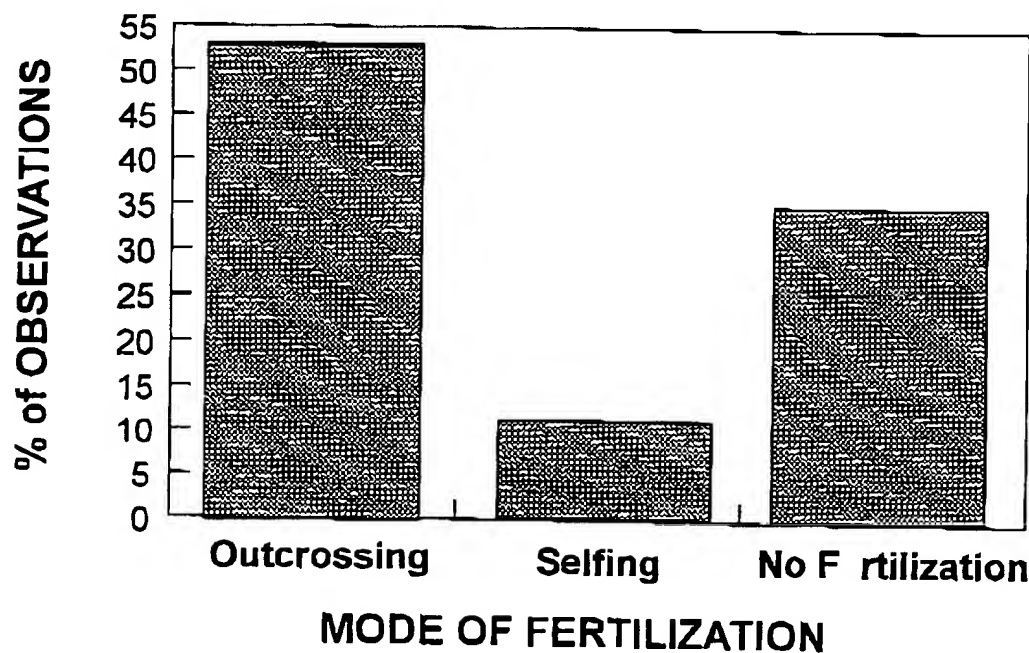

Fig. 3. Frequency of outcrossing, selfing, and lack of fertilization during two hour focal animal observations of pairs or trios of clam shrimp *Eulimnadia texana*. *N* = 178 groups.

After fertilization occurred (either due to selfing or outcrossing), males were returned to rearing tanks while the hermaphrodites were kept in isolation so that eggs could be collected. Eggs remained in the brood chamber for approximately 24 hours. Hermaphrodites were returned to the rearing tanks after they dropped their eggs. On one occasion, a hermaphrodite was seen dropping its clutch and then selfing another clutch within one hour.

Discussion

Sex ratios

The majority of Conchostracan species have a 50:50 sex ratio between males and females (Sassaman, 1989). The skewed sex ratio of *E. texana* can be attributed to the nature of sex determination for this system. Comparisons of sex ratios for thirteen *E. texana* populations across the United States showed an average sex ratio of approximately 75–80% hermaphrodites, 20–25% males (Sassaman, 1989). The sex ratio in the LTER playa is fairly characteristic for the species. One population, SWP3, was entirely hermaphroditic. The percentage of males within the SWP4 and SWP5 populations (40–42% respectively) are somewhat high when compared to the range of sex ratios in populations examined by Sassaman (range=0–35% males) (Sassaman, 1989).

Population genetics modeling of the *E. texana* breeding system has suggested that the costs associated with sexual reproduction would make the gradual elimination of males a natural occurrence if some type of inbreeding depression were not present to offset the benefits of selfing (Otto *et al.*, 1993). Sassaman (1989) reported probable all-hermaphrodite populations of *E. texana* in Florida and Texas. What makes the observed absence of males in SWP3 surprising, however, is the close proximity (35 m) of this population to other male-containing populations. Eggs of *E. texana* have a diameter of 220 µ (Belk, 1989) and could be dispersed by wind action or on the feet of cattle and birds that drink from the three small neighboring populations. If hermaphrodites bury their eggs within burrows, however, as current observations suggest, these mechanisms of dispersal may be limited in effectiveness. Other factors which maintain males within some of these *E. texana* populations and seemingly inhibit gene flow between these populations are as yet unknown.

The number of viable eggs hatching from the LTER playa population were significantly less than those hatching from the three SWP populations. Data are unavailable on the length of time *E. texana* eggs can remain viable in the field, but in general the population densities of all of the species living within the LTER Playa appear to decrease with an increase in length of time between floodings (MacKay *et al.*, 1990). The LTER Playa has not seen a significant flood in ten years (October, 1984) and this may account for lower hatch rates from this soil when compared to the samples taken from the other three populations. The SWP populations typically flood at least once every year and were flooded during the summers of 1992 and 1993 (pers. obs.). Also the LTER Playa clam shrimp share the playa with other ephemeral shrimp. These species may provide competition for food resources or predation pressures which lower *E. texana* population densities. Such pressures would be absent from the SWP populations because no other ephemeral shrimp live within these sites. The bare mud substrates of the SWP sites may also be better suited for clam shrimp burrowing and egg laying than the vegetated LTER Playa substrate.

The tadpole shrimp *Triops longicaudatus* also hatched within the LTER Playa rearing tanks. Previous research had suggested that the tadpole shrimp, *T. longicaudatus* only feeds on dead prey (Medland, 1989; MacKay *et al.*, 1990; Weeks, 1990; Loring, pers. comm.). This conflicts with the behavior of *T. longicaudatus*, in our laboratory where they were avid predators; thus all tadpole shrimp were removed from rearing tanks to avoid predation. When tadpole shrimp had been left within a tank, they ate all of the clam shrimp within a matter of days. Similar predation by *T. longicaudatus* has been reported for other laboratory populations of *E. texana* (Sassaman & Weeks, 1993). This may not occur as often in the field because *T. longicaudatus* typically remain near the bottom of a playa while *E. texana* remains around the periphery (Medland, 1989; pers. obs.). Tank size constraints in the laboratory may make contact between the two species more common and thus predation more prevalent.

Behavioral observations

This study supports several predictions of a recent population genetics model designed to study the relative costs of outcrossing and selfing (Otto *et al.*, 1993). One prediction of the model is that male mortality rates will be higher than hermaphrodite mortality rates. High

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male mortality rates relative to hermaphrodites within this study along with earlier field reports (Strenth, 1977) and general laboratory observations (Sassaman & Weeks, 1993) support this prediction. Secondly, Otto et al. (1993) predict that, unless inbreeding depression is quite high, levels of outcrossing must be high when males are present. In support of this prediction, although selfing was seen during these observations, it was comparatively rare (11%) compared to outcrossing (53% of observations). The close proximity of males and hermaphrodites in this artificial situation may, however, have contributed to the high level of outcrossing observed. The model also predicts that when males are absent, large numbers of eggs will go unfertilized. The current study found that hermaphrodites are gravid for a large percentage of their mature life span (72%) even as male numbers dwindle in the population. In order for the predictions to be correct, many of these selfed eggs must be infertile. Future studies should be designed to ascertain the relative fecundity of selfed versus outcrossed clutches.

During the instantaneous scan sampling, hermaphrodites were never seen dropping their clutches but there is some suggestion that they may deposit clutches within the burrows they dig. On several occasions during the initial observations, gravid hermaphrodites were seen digging a burrow and then emerging from it without their clutch. Non-gravid hermaphrodites and males were never seen digging burrows. During the focal animal observations, no substrate was provided so that all interactions between the clam shrimp would be visible and eggs could be collected. Absence of a substrate precluded observations of any digging behavior. During the scan sample observations, males were seen entering burrows. If hermaphrodites drop their clutch within a burrow, it seems likely that males might enter burrows in search of non-gravid hermaphrodites to mate guard prior to the hermaphrodites, next clutch.

Outcrossing behavior

This study provides the first detailed documentation of the sequence of events associated with outcrossing for *E. texana*. Molting appears to be necessary before fertilization is possible. This is a common occurrence in crustaceans (Ward, 1983). In many crustaceans, the correlation between molting and fertilization has limited the receptivity period of females and it has been suggested that this may lead to male/male competition for mates and mate guarding (Elwood et al., 1987; Anstensrud, 1992). The male's clasping and swimming with the hermaphrodite for extended periods suggests that precopulatory mate guarding exists within this species. Male clasping of gravid hermaphrodites provides further evidence for the occurrence of precopulatory mate guarding. In studies of other small crustacean species, mate guarding carries a variety of costs including high energy requirements, an increase in susceptibility to predation, and loss of time that could be spent searching for other females (Elwood & Dick, 1990). There may be similar costs related to mate guarding in *E. texana*, particularly relating to increases in energy demands since males push hermaphrodites around and fight off other males (see Knoll & Zucker, 1994).

The *E. texana* mating system provides an ideal opportunity to study the relative costs of sex and selfing. It is well known that outcrossing incurs the costs of sex. The maintenance of males in most populations of this species suggests that there must be costs to selfing as well. My observations suggest that the hermaphrodite can control the mode of fertilization (selfing *vs* outcrossing). Outcrossing was never observed between a male and a struggling hermaphrodite. There were instances in which the struggling hermaphrodite was much smaller than the clasping male and could not have physically forced him to release his grasp (pers. obs.). Instead, it appeared that males released the hermaphrodite upon its struggling. My results also suggest that there are time costs incurred by hermaphrodites that self. Once a hermaphrodite let a male clasp for more than one minute, it was committed to outcrossing which occurred an average of 27 minutes later. A hermaphrodite that selfed, however, remained motionless an average of 65 minutes prior to fertilization. Thus outcrossing occurred in less than half the time on average than selfing.

During careful examination of mating behavior, I failed to observe any indication of a spermatophore-type structure being transferred to the hermaphrodite. A previous study suggested that males transfer such a spermatophore-like package to the eleventh thoracic segment of the hermaphrodite during outcrossing (Strenth, 1977). If sperm were transferred in a spermatophore-like form, it may have been too small to be visible during these observations.

The unique mating system of *Eulimnadia texana* and its close relatives provides the potential for answering many intriguing questions on the evolution of sex. Toward that end, this contribution provides the first detailed description of the behavior of these organisms

with an emphasis on mating activities. Many questions about the reproductive behavior and physiology of this species remain to be answered.

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